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(*Ligia oceanica*)

A Study in Adaptations to Habitat

by

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THE SEA-SLATER, *LIGIA OCEANICA*: A STUDY IN ADAPTATIONS TO HABITAT.

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MANY a person, overturning a large slab of stone by the sea-beach, has been startled to discover the space underneath tenanted by a crowd of gigantic Slaters, which, hurrying helter-skelter in every direction from their disturbed retreat, scuttle with astonishing celerity into crevices between stones, or, in the absence of such convenient lairs, race headlong over the surrounding rocks to halt in some slight depression, where they lie rigid and motionless, but alert and ready at an instant's notice to dash off again. The size and agility of these lusty animals and the air of resolute determination with which each pursues his independent career, have over and over again communicated a shock of alarm to the unwary stranger. For all their apparent ferocity these giants of their clan are as innocent of mischief or possibility of doing harm as the most timid little Slater that creeps under the mortar of a wall or hides itself in a flower-pot, and should you succeed in catching a few, no easy task for a novice, you will find not only that they can be handled with impunity, but that they actually make charming and entertaining pets.

There is one unfailing method of becoming intimately acquainted with an animal, and that is to maintain it in captivity under conditions as nearly natural as possible. Almost all the facts here set down with regard to *Ligia* are the result of a study by the author of specimens kept, as a rule, miles from the sea and watched at odd hours of the day and of the night. But first of all let me tell you where to search for Ligia and, once you have secured your captives, how to keep them in full health, so that they will freely and unconcernedly exhibit their hundred-and-one odd traits of fascinating Slater behaviour.

NATURAL HABITAT OF THE SEA-SLATER.

Ligia lives on the seashore just above high-water mark and always on rough, rocky territory; it is not found on sand

or mud, and is even rare among the rounded boulders that are steeply piled in bays open to the full force of the waves. One never fails to find the animal, hiding singly or in small groups, in deep, fissured, rocky crevices near the upper tidal fringe, from which difficult retreats it can on occasion be dislodged by gentle titillation with a piece of wire bent at the point. Under loose, flat slabs of coarse sand-stone, should you luckily know of a locality heaped with such, they congregate in crowds. All they demand in the way of a den is that a certain degree of natural dampness should be conserved; free ventilation by dry wind they cannot endure. By day they lie in hiding, and at dusk they begin to emerge from their retreats, running silently but actively about the rocks in search of food, and taking exercise. In the south of England I have seen an occasional specimen wandering openly on piers and rocks by day; in the north of Scotland they are almost wholly nocturnal. Perhaps the greater number and the greater vigilance of the shore-birds in these last localities have led to the production of a more wary type, for as a dainty titbit their plump bodies are relished by fowl of all descriptions.

Conditions in Captivity.

For ease of observation an attempt was first made to keep them in a confectioner's bottle. On a smooth glass surface they tend to huddle in a mass, swarming over each other's backs, and, as they thus hang together in clusters, it is easy at any time to lift out a handful. When the bottle, a tall one, was laid on its side, some of the animals thus unceremoniously overturned would begin to move towards the mouth of the vessel. On the polished glass they made but sorry progress; the leaders in the race would be overhauled by others in the rear, which, crawling over their predecessors' backs, would thus impede their advance. Arrived at the inclined neck of the bottle, upward progress of the foremost was extremely difficult owing to the clawing mass adherent behind. The struggling behaviour of the crowd was ludicrously suggestive of a crush of jostling, elbowing human beings, yet it would be quite fallacious to

suppose that the Ligiæ were animated by any wild impulse of rivalry or of escape.

The animal needs a rough surface for foothold. Glass and glassy surfaces scarcely fall within its range of domestic experience, and on such a disconcerting pavement it clings to and walks over its fellows merely because they afford a better grasp for its feet. Each of its seven pairs of legs is armed at the extremity with two little hooks, arranged not side by side like the prongs of a fork but one nearer the body and the other at the extreme tip. Young animals have sharp hooklets on their feet, and, when put to the trial, can with difficulty just climb a vertical sheet of unglazed writing-paper. In a larger animal the hooks are blunt, and the owner may have trouble in scaling an upright sheet even of rough wrapping-paper. Our simple experiment teaches us that we should furnish an adequate foothold for our captives—and indeed when so provided they show no particular tendency to cling one to another; it also throws light on a circumstance that might otherwise cause wonder, namely, that in their natural habitat on the shore the full-grown greybeards of the species are more fastidious and discriminating in regard to the quarters they inhabit than are the youngsters. Ligia wanders only where it can move with confidence and security; consequently the seniors are strictly confined to rough territory, whereas the feet of the small fry can safely take them to regions, such as the smooth water-worn pebbles of the beach, where their parents no longer dare venture.

Slaters of all kinds, whether they live by the seashore or far inland, are unable to withstand prolonged exposure to dry air, and any receptacle in which Ligia is to be confined should have a well-adjusted cover. Ultimately a large biscuit tin with tightly fitting lid was chosen as the most convenient house for them. To provide moisture and at the same time to act as a suitable foothold, a piece of rag wrung out of a mixture of half tap- and half sea-water was spread over the bottom of the tin. With occasional ventilation, such as occurs at the odd times of observation, the air supply is quite adequate, and the occupants instead of resenting the darkness seem actually to prefer it.

Feeding Habits.

When a colony of captive animals is thus kept together the individuals are apt to eat each other, the victims being those recently moulted, which in their soft-bodied state are specially vulnerable. An endeavour was made to discover a suitable food for them—not altogether a simple task owing to the fact that they feed only by night or at least under cover of darkness. The writer has never seen a Ligia, however hungry it might be, in the act of consuming food, while observers who have sought to study the feeding habits of ordinary land Slaters have commented upon the same difficulty. As Ligia is frequently found occupying common quarters with Shorehoppers (*Orchestia*) and with a bluish-grey land Slater known as *Porcellio*, specimens of both these animals, living and dead, were tentatively provided as food. The Shorehoppers were eaten, the specimens of *Porcellio* left untouched. Pieces of cooked bacon and cooked chicken were likewise neglected. Then different varieties of vegetable food were provided. Land plants were wholly disregarded; seaweeds of the Bladderwrack or *Fucus* type were in cases of dire extremity gingerly consumed, but blades of Oar-weed or *Laminaria* were voraciously eaten; when these are provided Ligia relinquishes its cannibal habits and its proclivity to kill and eat *Orchestia*.

The homes they select for themselves on the beach are remarkably clean; one never finds them, for example, underneath the soft, glutinous, decomposing wrack cast up by the sea and left stranded along high-water mark; whence one would infer that they are, like pigs when left free to themselves, somewhat particular and nice in their habits. In captivity their quarters are apt to become soiled, and the simplest way to keep them clean is to have a spare house for them and to change their quarters from time to time. The spare domicile, let us say, stands dry and empty. Into this they are transferred by hand from the box previously in occupation, and here they are repeatedly flooded with sea-water so as to wash their skins, the polluted water being on each occasion drained away until it is seen to escape clear. The cloth which provides dampness is at the same

time well washed and replaced in the new tin. When in this way they have a bath and a change of quarters every two or three days they thrive amazingly and appear to be as happy and contented as in their natural haunts on the shore.

Affinities of the Sea-Slater.

Having settled the problem of keeping our charge in a healthy condition in captivity, let us now consider the animal more closely. It is a member of the extensive group of animals known as isopods, the great majority of which are wholly marine, many being first-class swimmers. The only terrestrial isopods are the Woodlice or Slaters. Now Ligia, unlike the other slaters, is never found far from the sea. Though its chosen line of habitation is at a slightly higher level than the water-washed beach, it never strays out of reach of the surf, being most abundant where the rocks are frequently drenched with spray. Since the belief prevails that all our land animals have sprung from aquatic ancestors, is it possible that Ligia is in the stage of undergoing slow and imperceptible change from a sea to a land life?

If we drop the animal into a bucket of water, it slowly sinks to the bottom, meantime making clumsy and utterly ineffectual efforts to swim by alternately bending and straightening its body. A Shorehopper (*Orchestia*) or a Sandhopper (*Talitrus*) similarly let fall, behaves in exactly the same way. The evidence is strong that the Hoppers at least have sprung from aquatic ancestors, yet all three animals are strangely unable to make any forward movement in the free aqueous element. One might well suppose that certain of the long succession of marine ancestors had, while still inhabitants of the sea, relinquished their swimming habits in favour of a crawling mode of existence, and that these special reptant accomplishments had in turn enabled or enticed each family group to emerge on the land. This supposition, which, be it said, has possible bearings on the much disputed origin of land vertebrates, is rendered no less likely when we find in salt pools on the upper beach another interesting and beautiful little isopod, *Jæra*, which, though entirely aquatic, yet progresses wholly by crawling.

Respiratory Adaptations.

The aquatic affinities of Ligia are indicated best of all by its organs of respiration. Like all the water-inhabiting isopods, it breathes by means of gills, which consist of thin plates, underneath the hinder or tail part of the body, arranged in succession from before backwards like the leaves of a book. Gills differ from lungs in that they freely project from the surface of an animal, whereas lungs, the common instrument of ærial respiration, are contained in pocket-like recesses of the body. The reason why lungs are thus concealed within the body is that the lining membrane of every type of breathing organ, whether lung or gill, has to remain moist to permit passage of the gases of respiration. Should the delicate membrane be effectually touched by drought, an accident that is prone to happen in the case of a freely projecting gill, the owner must inevitably die of asphyxiation, which in turn explains why Ligia is under the imperious necessity of shunning localities that are arid. In its adjustment to the exigencies of air surroundings *Porcellio* has advanced a stage further than *Ligia*, for examination has shown that some of its gill plates contain a system of hollow branching tubes into which dry air can diffuse with less risk of doing damage.

While the configuration of the breathing apparatus in itself indicates insufficient adaptation to land conditions, the behaviour of these gills during immersion is no less suggestive of an aquatic history. In orderly succession they beat the water with a beautifully regular and wavelike rhythm, by which action fresh supplies of fluid are constantly drawn over the respiratory surface. This active movement of the gills themselves, so characteristic of every aquatic isopod and so rare in other crustacean forms, is imperceptible so long as Ligia is surrounded by air. As the mechanism of the movement is highly intricate and involves the harmonious action of an elaborate system of nerves and muscles, it is incomparably simpler to suppose that Ligia has retained a pre-existing endowment than to believe that it has independently developed such an accomplishment merely to meet the contingency of occasional immersion.

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Suppose we immerse the animal in rain- or tap-water which by some special contrivance is kept well aerated. After some hours, while still active, it shows signs of swelling of the body; later its gill movements become irregular, and finally cease; its heart, which lies in the hinder part of the body and is visible through the skin of the back, may yet continue to beat for a time, but eventually, after a period varying from a few to forty-six hours, the animal succumbs. By applying a simple chemical test (silver nitrate) to the surrounding water the presence of abundant salt can be demonstrated; this must have leaked through the skin or gills of the animal, its eventual death being due to the loss of this salt.

Let us now vary the experiment by making the water a little salt. So soon as we mix sea-water with the rain-water, even to the extent of one-quarter dilution, the period of survival is considerably extended, and in proportion as we bring the salinity of the water up to that of the sea the animals live longer and longer. With complete immersion in aerated sea-water a well selected example may live without food for as long as three whole months. So close is the correspondence between the salinity of the sea and the bodily arrangements of Ligia, that, when one of the specimens plunged under fresh-water shows marked signs of distress—swelling of the body for example—on transference to sea-water the tumidity subsides and in a few hours the animal is none the worse for its unpleasant experience.

The remarkable result of these experiments proves at least that Ligia is a thoroughly amphibious animal; in point of fact it constantly enters the sea of its own free

will, which statement applies with particular validity to the young and tender forms. A further presumption is that, unlike other members of the groop of Woodlice, which succumb more quickly under sea- than under fresh-water, Ligia is in the direct line of descent from truly marine ancestors. We may recall that the food it eats is salty, and that it consistently refuses land-grown food; its blood too, which can be readily expressed from the antennæ, is very salt to the taste. In its bodily functions, therefore, as well as in its structure, it continues to bear indubitable marks of the primal ocean, and the specific name *oceanica*, chosen by Linnæus in 1767 for the common species of Northern Europe, thus proves to be singularly appropriate.

Adaptation and Distribution.

The length of time that the animal can endure complete immersion in salt-water may well provide the explanation of one fact that long puzzled the writer. Given adequate territory for habitation, it is found at every available spot round the length and breadth of our coasts. As it cannot directly cross a long stretch of intervening sand, the problem was to account for its never-failing presence wherever rocks and rocky crevices occur. The probability is that the creature, by clinging to floating wreckage or other wind-drifted material, is transported by sea; thus no recently bared, suitable locality could long remain devoid of a Ligian population. In these accidental migrations some must succumb by being carried bodily to sea, running imminent risk of death from ever watchful and predacious enemies (as bait for fishes Ligia is regularly used by the Japanese), but the chances are that occasional survivors will effect a successful landing, to carry on in virgin countries the traditions of their race. In adventurous voyages of such uncertain duration the high capacity of the animal for enduring famine, a characteristic it shares with many Crustacea, must be taken into account.

Any animal emerging from the sea and seeking to establish itself on land is confronted with a host of novel and exacting conditions. Apart from the all-important

evaporation question, there is the danger of occasional soaking with rain. As free contact with this element is apt to extract essential salts, Ligia is obliged to seek out dwellings with an impervious roof; should it be flooded out in a thunderstorm its one sure refuge is the sea. Only by gradual stages can its bodily economy become so modified that it can afford to wander out of reach of its primordial sanctuary, and we may feel sure that much water will yet run under the bridges ere it or its descendants enjoy the same free range over the land as is the privilege of its more familiar cousins, Porcellio and the rest of them.

Adaptations for Clinging.

We have already had occasion to note the persistency with which Ligia seeks out and clings to objects that afford suitable foothold. In studying its behaviour it was considered expedient to use sheets of sand-paper as a portable playground or race-course, and one of the first objects of inquiry was to see how the sea-slater behaves in a gale. A sheet of coarse sand-paper was pinned to the table and with the aid of an electric fan its surface was swept with a strong blast of air. When the hurricane was at its height a Ligia was let down upon the sand-paper and given a moment to adjust itself. Squatting flat, with its fourteen feet hooked on every *point d'appui*, the animal doggedly held its own and was not to be dislodged even with contributory pressure from the finger. When its feet on the weather side were tickled with a pencil, a somewhat unfair proceeding which corresponds to nothing that could well happen under similar circumstances in nature, it let go and was swept across the table, to drop lightly upon the floor below. A new device had now been brought into play; by bending its body the animal had rounded itself into a ball, and had it not escaped the draught it was prepared to continue its course by rolling.

When one bears in mind that some of the common marine isopods, for example *Idotea*, can on occasion flex their body into a sharp hook or loop, it is the less surprising to discover that Ligia can round itself into a fairly respectable ball. Among the isopods it has been reserved for certain

special members of the terrestrial group, the so-called "pill-bugs," to carry this art to its highest perfection, the common *Armadillidium vulgare*, on very slight provocation or hint of danger, curling itself into a perfect sphere, from which no single portion of body appendage projects. In Ligia this reaction is less common and the sphericity less complete, nor can the animal conceal its stout antennæ within the ball. Experiment showed that the posture is not assumed as a defensive reaction, but rather when the animal, either in full racing career or when jerked upwards on a stiff sheet of paper, temporarily loses its footing. On more than one occasion while hunting Ligia on slanting rocks, the author has seen the animals roll for a considerable distance and bounce from slope to slope. The pose is maintained just so long as the external agitation is continued, and the creature promptly uncurls itself when it comes to rest.

If we examine the under surface of the body we see that the seven pairs of legs are beautifully fitted for clinging. Transferring to Ligia the terms we use in speaking of our own anatomy, we may say that the "thighs" are set wide apart and that all the "knees" point towards the middle line of the body; the jointed leg below the knee then splays outwards to end in the immovable double claw. The front legs, which are short and reach forwards, have a backwardly directed "elbow" rather than a knee; the long hinder legs, which project backwards, have a forward pointing "knee." The consequence is that the terminal claws are arranged along the curved border of the animal from head to tail like so many boat-hooks held out from the side of a boat, and should the creature choose to hold fast it has the necessary tackle ready.

It seems strange that in such a fleet and active animal the hooks or claws on the posterior limbs should dig into the ground so as to resist not a backward thrust but a forward pull on the part of the leg. Suppose that we select from our tin a well-rested Ligia and place it on a sheet of sand-paper held horizontally in the hand, the head of the animal being directed to a distant edge of the sheet. So soon as we let it go it races off in a straight line, never

slackening speed for one instant as it approaches the dangerous precipice. It plunges over. We involuntarily look down, for we could have sworn that it fell. Yet it is not on the floor. When we examine the sand-paper we find our acrobat suspended side downwards from the edge, calmly engaged in making its further way at right angles to its previous course. The hind claws of Ligia are used in perilous descents over rocks, and when in full course it becomes necessary to draw up suddenly, this braking gear can be instantaneously thrown into action. At the same time it is worthy of note that, for all its provision of momentum-checking mechanism, nothing can induce Ligia to reverse its gait and walk backwards, which implies that the central nervous connections for this purpose are undeveloped.

Sensory Adaptations.

It has been said that the content of a dog's mind largely centres around olfactory sensations. Such consciousness as Ligia possesses of the external world must chiefly depend on impressions received from the ventral part of its body with its cluster of limbs. While the whole dorsal surface is dull and insensitive, each single limb is exquisitely endowed with sensation, the animal reacting by some special movement to the slightest touch on any ventral appendage. In full flight across a slab of rock Ligia will stop dead at any chance crack or depression, and squat. Without something to cling to, as in free water, the animal is deprived of its main source of sensory communication with the external world. In a three-dimensional universe it knows only two dimensions. Its power of orientation is related not so much to gravity as to a surface of some kind, and it is as much at home on the under surface or on the vertical face of a rock as on its upper surface. Just as a child from its inferior stature is more engrossed with objects at its feet than is a grown man, so in infinitely greater degree is Ligia's range of sensory experience limited to the surface with which it is for the moment in contact.

As an aid in exploration, its well-developed antennæ

are of notable service. Held outwards in front of the head, with the terminal portion drooping downwards, these are used in progression to probe the path exactly as a blind man uses a stick. It is true the animal has eyes, but it soon becomes evident that the eyes are useless for focussing or for judging distance. Suppose the cloth in the bottom of their house is arranged in the form of a peaked hill. The animals, wandering about the floor, climb to the top of this elevation and stand there probing the air with their feelers. Should the peak of the eminence be so near the side of the tin that the antennæ can bridge the gap, the Ligiæ immediately make efforts to clamber on to the side of the box. If the gap is adjusted to be ever so little greater, just enough to preclude contact by the antennæ, the animals remain utterly unaware of their proximity to the wall. Their eyes have therefore no clear vision like our eyes; at the same time they are eminently responsive to sudden variation in the size or position of shadows, as when one makes a movement.

Colour Change.

Unlike other terrestrial isopods, Ligia resembles some of the marine forms in being able to change its shade of colour in response to its surroundings. Specimens taken during the daytime from under stones on the beach vary somewhat in colour. The females are mottled, having laterally situated lighter patches on an otherwise uniformly dark ground, this mottling being still more conspicuous when the animals are viewed under water. Exposed to light in a black-painted dish the creatures retain their dark appearance. Exposed in a white dish they gradually grow lighter in colour and more transparent, so that eventually the heart can be seen beating through the integument over the back. The effect is equally pronounced when the experiment is carried out in the faint red light of a photographic darkroom, the specimens on a light background becoming light in shade, those on a dark becoming dark. When a Ligia is temporarily blinded by having its eyes

covered with black paint, it does not undergo the usual change of colour on transference to a white background, which shows that the reaction depends on the mode of illumination of the eyes. This power of colour change, long recognised as occurring in *Idotea*, and noted by the author in *Ligia*, in *Sphæroma* and presumably in *Glyptonotus*, is generally assumed to be a device for better concealment, though it is hard to admit this explanation of its purpose in Ligia.

One might go on recounting detail after detail with regard to this inadequately studied yet delightfully interesting animal; in particular its breeding habits, its moulting habits, its blood and its nervous organisation have afforded very pleasant holiday occupation to the writer. But already the account is unwarrantably long. Perhaps two outstanding points of interest concerning the animal may be emphasised: its beautiful adaptation to its own particular habitat, and the quite peculiar position it occupies as a presumptive transitional form between marine and terrestrial isopods.

The following communications contain further information and bibliographic references in regard to Ligia:—

[1] Hewitt, C. G., "Ligia," *L.M.B.C. Memoirs*, xiv., London, 1907, p. 37.

[2] Tait, J., "Colour Change in the Isopod, *Ligia oceanica*," *Journ. of Physiol.*, 1910, xl.; *Proc. Physiol. Soc.*, pp. 40-41.

[3] Tait, J., "Crustacean Blood Coagulation as Studied in the Arthrostraca," *Quart. Journ. Exper. Physiol.*, 1910, iii., pp. 1-20.

[4] Tait, J., "Types of Crustacean Blood Coagulation," *Journ. Marine Biol. Assoc.*, 1911, ix., pp. 191-198.

[5] Tait, J., "Capillary Phenomena observed in Blood Cells; Thigmocytes, Phagocytosis, Amœboid Movement, Differential Adhesiveness of Corpuscles, Emigration of Leucocytes," *Quart. Journ. Exper. Physiol.*, 1918, xii., pp. 1-33.

[6] Tait, J., "Immersion Experiments on Ligia," *Proc. Roy. Soc. Edin*, 1917, xxxvii., pp. 50-58.

[7] Tait, J., "Moulting of Isopods," *Proc. Roy. Soc. Edin.*, 1917, xxxvii., pp. 59-68.

[8] Tait, J., "Limb-Flexures and Limb-Taxis in the Peracarida," *Proc. Roy. Soc. Edin.*, 1917, xxxvii., pp. 69-94.

[9] Tait, J., "Some Structural Features pertaining to Glyptonotus," *Proc. Roy. Soc. Edin.*, 1917, xxxvii., pp. 246-303.

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OLIVER AND BOYD, EDINBURGH